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RECRUITMENT OF *FRAXINUS PENNSYLVANICA* (OLEACEAE) IN EASTERN MONTANA WOODLANDS

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ABSTRACT

Fraxinus pennsylvanica Marsh. (Oleaceae) woodlands are an important habitat for conservation of biological diversity on the Northern Great Plains. Many *F. pennsylvanica* woodlands appear to lack tree regeneration; however, little is known about the mode of recruitment in these stands. I sampled species composition, seedling density and the extent of vegetative recruitment of *F. pennsylvanica* for 17 stands in east-central Montana. Stand age distributions indicate that recruitment during the past 50 years has been greatly reduced compared to the previous 50 years. Detrended Correspondence Analysis identified a strong gradient in species composition positively associated with canopy cover of tall shrubs and mean annual precipitation and negatively associated with exotic grasses. Seedling recruitment of *F. pennsylvanica* was more common in stands with high DCA scores. The frequency of multi-stem tress indicated that at least 30% of *F. pennsylvanica* trees arose vegetatively. Rejuvenating sparse *F. pennsylvanica* woodlands should include both vegetative and seedling tree recruitment. Burning and/or cutting old, diseased trees with sparse canopies could create more vigorous stands once the sprouts have matured. Shadier habitat of such stands may encourage seedling recruitment by reducing the vigor of sod grasses.

Fraxinus pennsylvanica Marsh woodlands are found along small-order drainages and on moist, cool slopes throughout much of the eastern third of Montana as well as most of the Northern Great Plains. Although *F. pennsylvanica* woodlands comprise only a small proportion of this prairie landscape, their aesthetic, economic and biological values are large compared to their aerial extent (Noble and Winokur 1984). Many species of plants and animals occur only in habitat provided by *F. pennsylvanica* woodlands. For example, Faanes (1984) recorded 47 species of breeding birds in western North Dakota woodlands, 22 of which were neotropical migrants. Of the 81 species of birds observed in *F. pennsylvanica* woodlands by Rumble and Gobeille (1998), 65 require woodland habitat. Lesica (1989) lists several vascular plant species occurring in eastern Montana only or primarily in *F. pennsylvanica* woodlands.

Unfortunately, evidence from throughout the Northern Great Plains suggests that tree recruitment has declined in many *F. pennsylvanica* woodlands (Boldt et al. 1978; Lesica 1989). Woodlands with dense, stratified canopies and undergrowth dominated by native shrubs, graminoids, and forbs are being replaced by open canopy communities with few tall shrubs in the understory and a ground layer dominated by introduced sod-forming grasses (Hansen and Hoffman 1988). Many native animals decline as woodlands become more open. Bird density and diversity was lower in these open-canopy stands in northwestern South Dakota (Hodorff et al. 1988; Rumble and Gobeille 1998). Deer mice (*Peromyscus maniculatus*), white-footed mice (*Peromyscus leucopus*) and woodrats (*Neotoma cinerea*) occurred more commonly in closed-canopy stands, while no mammalian species was more common in the open stands (Hodorff et al. 1988).

It is imperative to maintain existing closed canopy *F. pennsylvanica* woodlands and restore open stands in order to maintain biological diversity of the Northern Great Plains. Management and restoration of these woodlands hinges on understanding tree recruitment. *Fraxinus pennsylvanica* reproduces from seed and by vegetative sprouting from the tree base (Hansen et al. 1984; Uresk and Boldt 1986; Lesica 1989; Sieg and Wright 1996). However, the past and present importance of these two modes of recruitment in native woodlands is not known. In this study I measured current levels of vegetative and seedling recruitment in relation to current stand condition to help determine what environments are conducive to recruitment. I also obtained age-class distributions from increment core data to gain insight into past recruitment regimes. Results are used to develop restoration and management strategies.

STUDY SITES

I conducted my study at six sites in Custer, Dawson, Fallon, McCone, Prairie and Wibaux counties in east-central Montana (Fig. 1). Elevations of the study sites range from 745 m at Fort Peck to 1005 m at Cedar Creek. Soils are derived from soft sandstones, siltstones and claystones of the late Cretaceous Fort Union Formation (Veseth and Montagne 1980). Climate of the study area is semi-arid and continental. Mean annual precipitation ranged from 29 cm at Fort Peck to 41 cm between Baker and Wibaux (USDA-SCS 1981). Mean January minimum and July maximum temperatures at Terry in the center of the study area were $-18°$ and 31°C respectively (NOAA 1982). Mean annual precipitation for the study areas was derived from a map

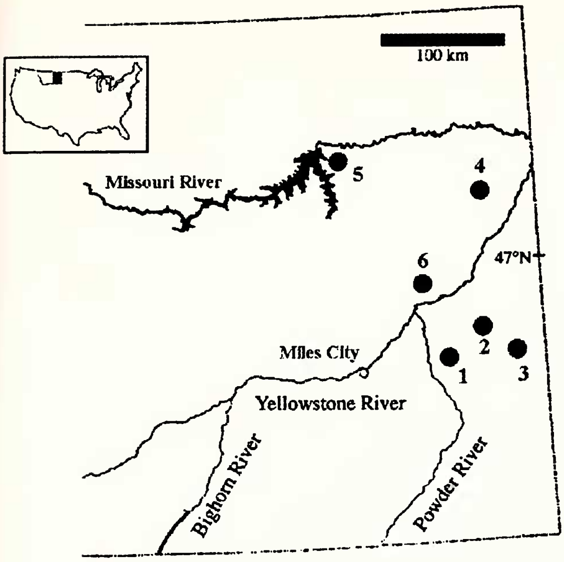

FIG. 1. Location of six study sites in east-central Montana: (1) Rattlesnake Butte, (2) Cabin Creek, (3) Wibaux, (4) Bible Camp, (5) Fort Peck, (6) Cedar Creek.

of precipitation isohyetal lines for Montana for the period 1941-1970 (USDA-SCS 1981).

Upland vegetation of the study area is steppe dominated by *Artemisia tridentata* ssp. *wyomingensis* Beetle and Young and perennial grasses including *Stipa comata* Trin. and Rupr., *Agropyron smithii* Rydb. and *Bouteloua gracilis* (H. B. K.) Griffiths Woodland vegetation dominated by *F. pennsylvanica* occurs in narrow bottomlands along ephemeral drainageways dissecting the uplands. These "woody draws" often occur at the head of drainage basins but may be found along channels farther downstream as well.

SPECIES DESCRIPTION

Fraxinus pennsylvanica is a small, dioecious, deciduous tree to 20 m tall and 50 cm in diameter in Montana. It is shallow rooted and common along streams and in floodplains and other bottomland habitats from Nova Scotia to Alberta south to Texas and Florida (Great Plains Flora Association 1986; Farrar 1995). *Fraxinus pennsylvanica* is reported to have a short-lived seed bank (Farrar 1995). Seedlings grow equally well in sun or shade (Borger and Kozlowski 1972). Wood is hard and was extensively cut for firewood, especially in the prairie states (Peattie 1953). Maximum age is thought to be ca. 100 years (Farrar 1995) Montana plants are sometimes considered to be var. *lanceolata* or var. *subintegerrimus,* but these varieties are now considered of little taxonomic value (Great Plains Flora Association 1986).

METHODS

Field methods. I sampled 17 stands among the six study sites. Stands were stratified by county and selected randomly from a list of stands managed by the USDI Bureau of Land Management. Only stands more than 2 ha in extent with *Fraxinus pennsylvanica* canopy cover reported to be at least 40% were included in the original pool of stands.

After thorough reconnaissance, I subjectively located a 50 × 20 m sample plot to represent each stand. I estimated total tree canopy cover with a spherical densiometer at 12.5 and 37.5 m along the center line of each plot. I also recorded ocular estimates of canopy cover of all woody plants and all herbaceous plants with cover of 1% or more. Vascular plant nomenclature follows Great Plains Flora Association (1986).

In each plot I recorded the total number of trees equal to or greater than 2 m high into five 10-cm size classes by species. I tallied all trees in the sample plot into size classes and noted the presence of multiple stems and trunk sprouts (shoots arising vegetatively from the tree base) for all trees. Density of tree seedlings (stems <2 m tall and ≤10 yrs old not arising from an older plant) was estimated from four 20 m^2 or 50 m^2 circular subplots equidistant along the macroplot center line. Larger subplots were used when seedling density was low.

I obtained the age, diameter and height of one randomly chosen sample tree of each species in each size class in each quarter-section of each plot. I estimated the height of sample trees to the nearest 0.5 m with a 3-m gauging pole. Diameter was measured to the nearest 1 cm with a tape. Age was obtained from increment cores taken at 0.5 m above ground level. The number of annual rings was counted using a 10–20× microscope with cross-dating to help assure accuracy (Stokes and Smiley 1996). This method could underestimate the true age if tree stems were less than 0.5 m for one or more years. Several sample trees had rotten centers, and age could not be determined. Diameter of multiple-stem trees was calculated as the diameter of a single-stem tree of equivalent basal area.

Data analysis. Stand-level basal area of tree species was estimated by assigning the midpoint of each diameter size class to all trees in that class. I used the coefficient of variation (cv, standard deviation/mean) as a measure of how evenly distributed tree ages were within stands.

I ordinated common species and stands using Detrended Correspondence Analysis (DCA; Gauch 1982; Rasmus 2000) to elucidate environmental gradients important to recruitment. Canopy cover estimates of all species present in at least five stands were used as input (McCune and Mefford 1997).

I used regression analysis to test the significance of associations between precipitation and vegetation (DCA score) and the proportions of trees with

TABLE 1. FREQUENCY OF OCCURRENCE, MEAN PERCENT CANOPY COVER AND DCA AXIS 1 SCORES FOR COMMON (FREQUENCY >25%) SPECIES IN 17 SAMPLE STANDS.

	Frequency	% cover	DCA score
Trees			
Acer negundo	7	2	233
Fraxinus pennsylvanica	17	37	120
Shrubs			
Amelanchier alnifolia	7	1	211
Prunus americana	6	1	226
Prunus virginiana	15	16	243
Ribes setosum	12	<1	20
Rosa woodsii	10	1	−18
Symphoricarpos occidentalis	14	12	26
Toxicodendron rydbergii	6	1	138
Graminoids			
Agropyron repens	5	3	81
Bromus inermis	7	9	−91
Bromus japonicus	6	8	24
Carex sprengelii	5	14	323
Poa pratensis	15	26	−14
Forbs			
Achillea millefolium	5	<1	−26
Arctium minus	6	1	269
Cystopteris fragilis	6	<1	288
Disporum trachycarpum	6	<1	169
Galium aparine	11	1	289
Galium boreale	6	<1	161
Hackelia deflexa	6	<1	162
Monarda fistulosa	5	<1	27
Ranunculus abortivus	6	<1	273
Smilacina stellata	10	2	158
Smilax herbacea	7	<1	120
Taraxacum officinale	8	4	12
Thalictrum spp.	10	<1	252
Viola canadensis	5	<1	69

trunk sprouts and multiple stems and between seedling density and precipitation, vegetation and cv of tree age. I used Analysis of Variance (ANOVA) to test the effect of the presence of multiple stems and trunk sprouts on tree age and size. Mixed models included site and an interaction term as factors. The main effect was tested against the interaction term when the latter was significant ($P \leq 0.10$).

RESULTS

Stand descriptions. Fraxinus pennsylvanica woodlands had total tree canopy cover of 18% to 73% with a mean of 45%. *Fraxinus pennsylvanica* was the dominant tree in all stands. Basal area ranged from 5.6 m^2/ha to 37.5 m^2/ha with a mean of 14.9 m^2/ha, and mean canopy cover was 37% (SE = 4%). *Acer negundo* L. (boxelder) occurred in six stands with a mean basal area of 2.2 m^2/ha and mean canopy cover of 7%. *Ulmus americana* L. (American elm) occurred in three of the four easternmost stands with a mean basal area of 5.7 m^2/ha and a mean canopy cover of 22%.

Fraxinus pennsylvanica trees were 2.0 to 14.5 m tall with a mean of 7.0 m (N = 204, SE = 0.2 m) and basal diameters of 2.5 to 65 cm with a mean of 23 cm (n = 227, SE = 1 cm). *Ulmus americana* occurred in three sample stands at the Wibaux and Bible Camp sites. Diameter of *U. americana* ranged from 7 cm to 68 cm with a mean of 25 cm (N = 20, SE = 3 cm). Height varied from 5 m to 14 m with a mean of 9 m (SE = 0.5 m). I sampled only 10 *Acer negundo* trees, all of which were at the Cabin Creek and Wibaux sites. Diameter ranged from 20 cm to 50 cm with a mean of 30 cm (n = 10, SE = 3 cm). Height ranged from 6 m to 13 m with a mean of 8 m (n = 8, SE = 1 m).

Detrended Correspondence Analysis (DCA) identified one strong gradient; axis 1 accounted for 64% of the variation in species composition. Species with low scores for DCA axis 1 included introduced rhizomatous grasses, *Bromus inermis* Leyss. and *Poa pratensis* L. as well as the low shrubs, *Symphoricarpos occidentalis* Hook. and *Rosa woodsii* Lindl. The weedy forbs, *Achillea millefolium* L. and *Taraxacum offiicinale* Weber also had low scores (Table 1). Species at the high end

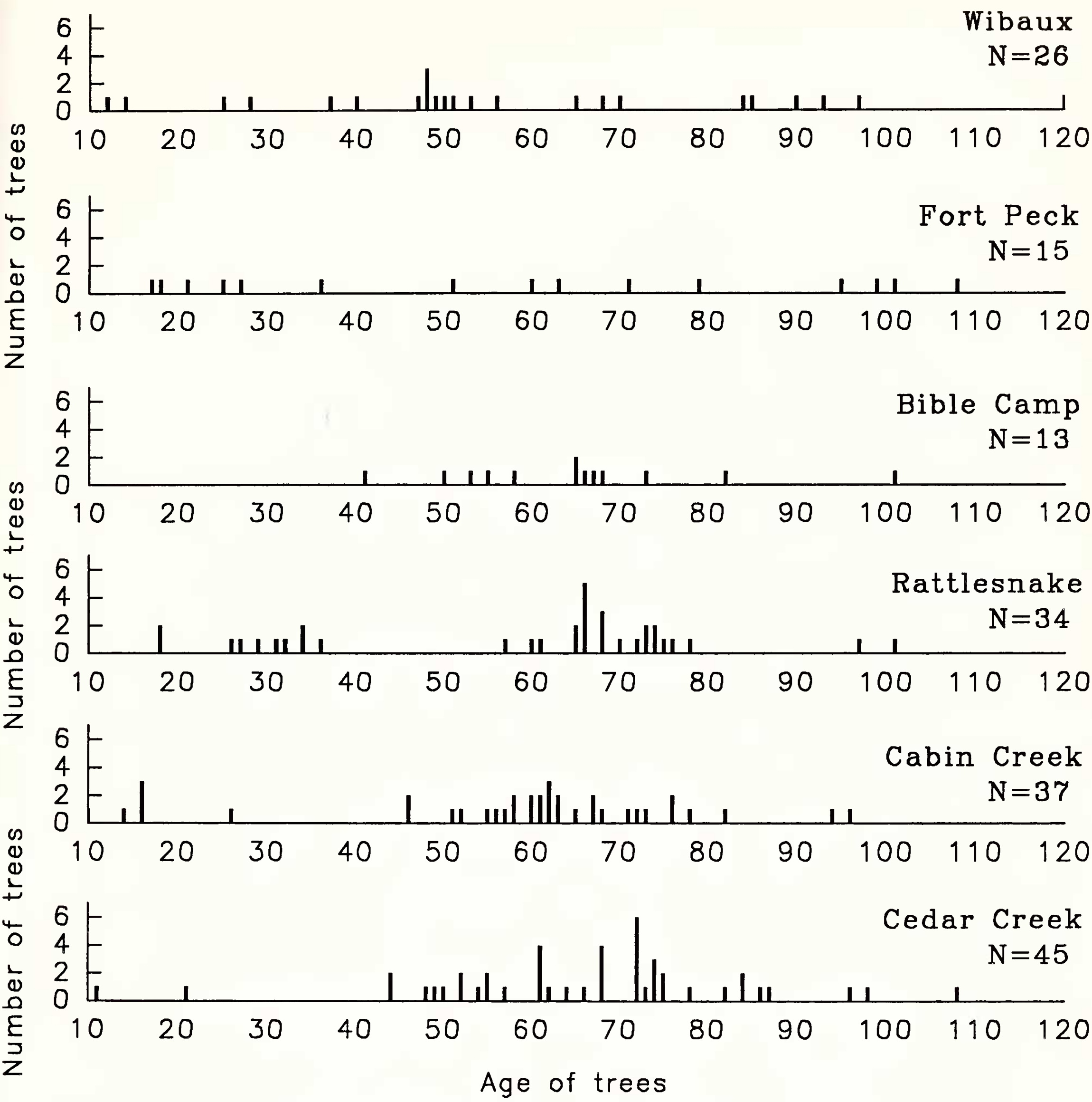

FIG. 2. Age distribution of *Fraxinus pennsylvanica* at six study sites in east-central Montana.

of DCA axis 1 include the tall shrubs *Prunus virginiana* L., *P. americana* Marsh and *Amelanchier alnifolia* Nutt. The highest score was assigned to *Carex sprengelii* Dewey, a native graminoid. Common forest species, *Galium aparine* L., *Cystopteris fragilis* (L.) Bernh., *Ranunculus abortivus* L. and *Thalictrum* spp. and the mesic-loving exotic, *Arctium minus* Bernh., also had high scores (Table 1). Stands with high DCA scores had higher mean annual precipitation ($R^2 = 0.26$, $P = 0.036$). Canopy cover of tall *Prunus* spp. ranged from 0% to 65% and was negatively correlated with the canopy cover of introduced rhizomatous grasses which ranged from 0% to 86% ($r = 0.58$, $P = 0.016$). Higher DCA scores were associated with lower canopy cover of exotic species ($R^2 = 0.80$, $P < 0.001$), and a model with both precipitation and cover of exotics explained 86% of the variation in vegetation ($P < 0.001$).

Recruitment. Fraxinus pennsylvanica, Ulmus americana and *Acer negundo* all reproduced both vegetatively and from seed in study plots. However, sample sizes were large only for *F. pennsylvanica,* so results and discussion will be limited to this species.

Age distributions of *F. pennsylvanica* trees indicate that most stands were not even-aged, and recruitment was sporadic (Fig. 2). A disproportionately large number of *F. pennsylvanica* trees in sample stands were 60–75 years old. Over all sites, 39% of the *F. pennsylvanica* trees regenerated in the 15-year period of 1926–1940. Only 27% (n = 173) of the *F. pennsylvanica* trees sampled were 50 years or younger, and only 3% were 100 years or older.

An average of 33% of *F. pennsylvanica* trees in study stands had live sprouts at their base, and 30% had more than one bole, indicating that they arose as basal trunk sprouts. Sprouting trees were larger than trees without sprouts with a mean diameter of 24 cm (SE = 1 cm) compared to 20 cm (SE = 1 cm; $F_{1,206} = 8.7$, $P = 0.003$). However, the mean age of sprouting and non-sprouting trees did not differ ($P = 0.296$). Multi-stem trees averaged 64 years (SE = 3 yrs) compared to 58 years (SE = 2 yrs) for single-stem trees ($F_{1,158} = 4.0$, $P = 0.05$). The abundance of multi-stem and sprouting trees was not associated with vegetation ($P > 0.62$).

Fraxinus pennsylvanica seedlings were uncommon in most stands. Mean number of seedlings per 100 m^2 was 10 (SE = 5). Nine of 17 stands (53%) had one or fewer seedlings per 100 m^2, and seedlings were entirely absent from sample plots in five stands. There was no association between mean annual precipitation and seedling density ($R^2 = 0.02$, $P = 0.58$). However, higher seedling density was associated with more mesic vegetation (high DCA axis 1 scores; $R^2 = 0.23$, $P = 0.05$), and this association was due more to a positive correlation with canopy cover of *Prunus* spp. ($r = 0.71$) than a negative correlation with exotic rhizomatous grasses ($r = -0.39$). Stands in which tree ages were more evenly distributed (as measured by the coefficient of variation for age) tended to have more seedlings ($R^2 = 0.22$, $P = 0.06$).

Discussion

The age structure of *Fraxinus pennsylvanica* stands indicates that recruitment in the second half of the past century has been low relative to the first half. Nearly 75% of *F. pennsylvanica* trees in sample stands were 50 years or older. *Fraxinus pennsylvanica* stems rarely persist more than 100 years on the Northern Great Plains (Butler and Goetz 1984; Girard 1985; Hansen et al. 1984; Hansen and Hoffman 1988; Farrar 1995; Sieg 1991) so density of *F. pennsylvanica* stems will decline by 50% over the next 50 years under current levels of recruitment.

Sprouting from the base of the trunk is an important mode of reproduction in *F. pennsylvanica.* A minimum of 30% of the trees in our sample stands arose as basal trunk sprouts, and vegetative reproduction occurred regardless of differences in associated vegetation. Although sprouting ability may be a function of tree size, younger trees were not more likely to sprout than older trees. More than 90% of *F. pennsylvanica* sprouted after being cut in an experiment in North Dakota (Uresk and Boldt 1986), although it is not known what proportion of these survived to become trees.

The large pulse of *F. pennsylvanica* recruitment that occurred between 1926 and 1940 may well have been due to trunk sprouting. Many trees were cut down by the large influx of homesteaders during the years of 1900–1918 (Malone and Roeder 1976). Starting around 1920 a decline in farm prices and a series of severe droughts led to a rapid reduction in the rural population (Malone and Roeder 1976) and a concomitant lessening of woodcutting and livestock numbers (Lee and Williams 1964), undoubtedly leading to lower woodcutting and grazing pressure. Interviews with long-time residents indicate that fire was not a significant factor (Lesica and Atthowe 2001). However, *F. pennsylvanica* may have responded directly to the drought conditions of the mid-1920's and 1930's by dying back to the ground and resprouting (Albertson and Weaver 1945). It is conceivable that whole stands rejuvenated during this time by trunk sprouting alone. However, it seems unlikely that *F. pennsylvanica* woodlands can persist over the long term relying solely on vegetative reproduction to provide a tree canopy.

Fraxinus pennsylvanica stands with higher densities of tree seedlings tended to have a greater array of tree ages, suggesting that steady recruitment from seed produced more uneven age structures than sporadic vegetative recruitment following drought, woodcutting or fire. However, *F. pennsylvanica* seedlings were uncommon in most stands and entirely absent from five of 17 sample plots. Lack of recruitment from seed during the past 50 years or longer has probably contributed to the skewed age distributions of most sample stands.

Fraxinus pennsylvanica woodland vegetation occupied a gradient from stands dominated by sun-loving, exotic grasses, grassland forbs and low shrubs to those with more closed understories dominated by *Prunus virginiana, P. americana, Amelanchier alnifolia, Carex sprengelii* and shade-loving forbs. Several other researchers have observed the same gradient in Montana and the Dakotas (Butler and Goetz 1984; Girard et al. 1987; Hansen and Hoffman 1988; Hodorff et al. 1988; Lesica 1989; Vorhees and Uresk 1992). Recruitment of tree seedlings was higher beneath more closed understories. The gradient defined by DCA axis 1 was associated with increasing mean annual precipitation, and decreasing canopy cover of exotic species. Abundance of exotics is frequently associated with level of disturbance, especially by livestock (Parker et al. 1993; Kotanen et al. 1998; Smith and Knapp 1999). Woodlands receiving more precipitation may be more resilient to grazing disturbance (Fahnestock and Detling 1999). Assuming that canopy cover of exotic species is a surrogate for disturbance, these results suggest that drought stress and overgrazing disturbance work in concert to favor stands with a more xeric, meadow-like understory, less conducive to tree seedling recruitment.

The association between density of seedlings and more mesic, less disturbed stands characterized by a high canopy cover of *Prunus* spp. and lower abundance of rhizomatous grasses suggests that recruitment of *F. pennsylvanica* from seed may depend on facilitation by a tall shrub understory. Reduced vigor of sod grasses associated with shading by a healthy shrub layer would likely mean more safe sites for tree seedlings (Albertson and Weaver 1945; Petranka and McPherson 1979; Van Auken and Bush 1997). In addition, *F. pennsylvanica* seedlings are very shade-tolerant (Borger and Kozlowski 1972), so interference from the *P. virginiana* canopy may be minimal. Tree seedlings may also experience a more humid environment and less herbivory under a shrub canopy (Callaway 1992, Werner and Harbeck 1982). The relationship between *P. virginiana* and tree recruitment could be pivotal to succession from a meadow/low shrub community to *F. pennsylvanica* woodland. Facilitation of *F. pennsylvanica* recruitment by *Prunus* species in these woodlands is plausible but requires experimental study for verification.

Recruitment of trees both vegetatively and from seed has been important in *F. pennsylvanica* woodland dynamics in the past. Rejuvenating open green ash woodlands is likely best accomplished by encouraging tree recruitment through both of these modes. Uresk and Boldt (1986) rejuvenated western North Dakota *F. pennsylvanica* woodlands by cutting decadent trees. Nearly all the trees sprouted after cutting. Prescribed fire may also be useful in encouraging vegetative recruitment of trees; low-intensity experimental burns induced sprouting of *F. pennsylvanica* in northwestern South Dakota (Sieg and Wright 1996). Burning and/or cutting old, diseased trees with sparse canopies could eventually create stands with greater canopy leaf area once the sprouts have matured. Tall shrub densities may also increase in stands exposed to fire (Zimmerman 1981). Shadier habitat of stands rejuvenated by cutting or fire should encourage seedling recruitment by reducing the vigor of rhizomatous sod grasses. However, fire could increase the abundance of exotic grasses in the short term by decreasing shade and increasing nutrient availability (Blair 1997).

These proposed restoration methods need to be tested in controlled experiments with livestock grazing excluded. Cattle will use woodland habitat heavily during the growing season (Boldt et al. 1978), resulting in lower canopy cover of tall shrubs (Butler and Goetz 1984; Hansen and Hoffman 1988). Tree sprouts grew taller, and survival of planted *F. pennsylvanica, Prunus virginiana* and *P. americana* was higher in ungrazed stands compared to stands grazed by cattle (Uresk and Boldt 1986). Further studies on the effects of tall shrubs and fire on seedling recruitment are needed.

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LITERATURE CITED

ALBERTSON, F. W. AND J. E. WEAVER. 1945. Injury and death or recovery of trees in prairie climate. Ecological Monograph 15:395–433.

BLAIR, J. M. 1997. Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. Ecology 78:2359–2368.

BOLDT, C. E., D. W. URESK, AND K. E. SEVERSON. 1978. Riparian woodlands in jeopardy on the northern High Plains. Pages 184–189 *in* R. R. Johnson and J. F. McCormick (eds.), Proceedings of the national symposium on strategies for protection and management of floodplain wetlands and other riparian ecosystems. USDA Forest Service General Technical Report WO-12. Washington D.C.

BORGER, G. A. AND T. T. KOZLOWSKI. 1972. Effects of light intensity on early periderm and xylem development in *Pinus resinosa, Fraxinus pennsylvanica,* and *Robinia pseudoacacia.* Canadian Journal of Forest Research 2:190–197.

BUTLER, J. AND H. GOETZ. 1984. Influence of livestock on the composition and structure of green ash communities in the Northern Great Plains. Pp. 44–49 *in* D. L. Noble and R. P. Winokur (eds.), Wooded draws: characteristics and values for the Northern Great Plains. South Dakota School of Mines and Technology, Rapid City.

CALLAWAY, R. M. 1992. Effect of shrubs on recruitment of *Quercus douglasii* and *Q. lobata* in California. Ecology 73:2118–2128.

FAANES, C. A. 1983. Breeding birds of wooded draws in western North Dakota. Prairie Naturalist 15:173–187.

FAHNESTOCK, J. T. AND J. K. DETLING. 1999. Plant responses to defoliation and resource supplementation in the Pryor Mountains. Journal of Range Management 52:263–270.

FARRAR, J. L. 1995. Trees in Canada. Fitzhenry & Whiteside, Markham, Ontario Canada. 502 pp.

GAUCH, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, UK.

GIRARD, M. M. 1985. Native woodland ecology and habitat type classification of southwestern North Dakota. Ph.D. dissertation, South Dakota State University, Brookings.

———, H. GOETZ, AND A. J. BJUGSTAD. 1987. Factors influencing woodlands of southwestern North Dakota. Prairie Naturalist 19:189–198.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence.

HANSEN, P. L. AND G. R. HOFFMAN. 1988. The vegetation of the Grand River/Cedar River, Sioux, and Ashland Districts of the Custer National Forest: a habitat type classification. USDA Forest Service General Technical Report RM-157, Fort Collins.

———, ———, AND A. J. BJUGSTAD. 1984. The vegetation of Theodore Roosevelt National Park, North Dakota: a habitat type classification. USDA Forest Service General Technical Report RM-113. Fort Collins, CO.

HODORFF, R. A., C. H. SIEG AND R. L. LINDER. 1988. Wildlife response to stand structure of deciduous woodlands. Journal of Wildlife Management 52:667–673.

Kotanen, P. M., J. Bergelson and D. L. Hazlett. 1998. Habitats of native and exotic plants in Colorado shortgrass steppe: a comparative approach. Canadian Journal of Botany 76:664–672.

Lee, B. and D. Williams. 1964. Last grass frontier. The South Dakota stock grower heritage. Black Hills Publishers, Sturgis, SD.

Lesica, P. 1989. The vegetation and condition of upland hardwood forests in eastern Montana. Proceedings of the Montana Academy of Sciences 49:45–62.

———, and H. E. Atthowe. 2001. Tree recruitment, disease and insect pests of green ash woodlands in east-central Montana. Unpublished report, USDI Bureau of Land Management, Miles City, MT.

Malone, M. P. and R. B. Roeder. 1976. Montana a history of two centuries. University of Washington Press, Seattle.

McCune B. And M. J. Mefford. 1997. PC-ORD. Multivariate analysis of ecological data, version 3.0. MjM Software Design, Gleneden Beach, OR.

National Oceanic and Atmospheric Association. 1982. Monthly normals of temperature, precipitation and heating and cooling degree days. Montana, 1951–1980. National Climate Center, Ashville, NC, USA.

Noble, D. L. and R. P. Winokur (eds.). 1984. Wooded draws: characteristics and values for the Northern Great Plains. Great Plains Agricultural Council Publication No. 11, South Dakota School of Mines and Technology, Rapid City.

Parker, I. M., S. K. Mertens and D. W. Schemske. 1993. Distribution of seven native and two exotic plants in a tallgrass prairie in southeastern Wisconsin: the importance of human disturbance. American Midland Naturalist 130:43–55.

Peattie, D. C. 1953. A natural history of western trees. Houghton Mifflin Co., Boston MA, USA.

Petranka, J. W. and J. K. McPherson. 1979. The role of *Rhus copallina* in the dynamics of the forest-prairie ecotone in north-central Oklahoma. Ecology 60:956–965.

Rasmus, E. 2000. Can we trust gradients extracted by detrended correspondence analysis? Journal of Vegetation Science 11:565–572.

Rumble, M. A. and J. E. Gobeille. 1998. Bird community relationships to succession in green ash (*Fraxinus pennsylvanica*) woodlands. American Midland Naturalist 140:372–381.

Sieg, C. H. 1991. Ecology of bur oak woodlands in the foothills of the Black Hills, South Dakota. Ph.D. dissertation, Texas Tech University, Lubbock.

———, and H. A. Wright. 1996. The role of prescribed fire in regenerating *Quercus macrocarpa* and associated woody plants in stringer woodlands in the Black Hills, South Dakota. International Journal of Wildlands Fire 6:21–29.

Smith, M. D. and A. K. Knapp. 1999. Exotic plant species in a c_4-dominated grassland: invasibility, disturbance and community structure. Oecologia 120:605–612.

Stokes, M. A. and T. L. Smiley. 1996. An introduction to tree-ring dating. University of Arizona Press, Tucson.

Uresk, D. W. and C. E. Boldt. 1986. Effects of cultural treatments on regeneration of native woodlands on the northern High Plains. Prairie Naturalist 18:193–202.

USDA-SCS. 1981. Average annual precipitation. Montana. USDA Soil Conservation Service, Bozeman, MT.

Van Auken, W. and J. K. Bush. 1997. Growth of *Prosopis glandulosa* in response to changes in aboveground and belowground interference. Ecology 78:1222–1238.

Veseth, R. and C. Montagne. 1980. Geologic parent materials of Montana soils. Montana Agricultural Experiment Station Bulletin 721, Bozeman, MT.

Voorhees, M. E. and D. W. Uresk. 1992. Relating soil chemistry and plant relationships in wooded draws of the Northern Great Plains. Great Basin Naturalist 52:35–40.

Werner, P. A. and A. L. Harbeck 1982. The pattern of tree seedling establishment relative to staghorn sumac cover in Michigan old fields. American Midland Naturalist 108:124–132.

Zimmerman, G. M. 1981. Effects of fire upon selected plant communities in the Little Missouri Badlands. M.S. Thesis, North Dakota State University, Fargo.